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SHORT COMMUNICATION

Dead frond "skirts" as tree fern defence: what is the evidence?

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Abstract: Many tree fern taxa have a skirt, an encircling structure of persistent dead fronds or stipes around the growing crown at the top of the trunk. Page and Brownsey (1986) hypothesised that the function of these skirts was to protect tree ferns against damage from large epiphytes, hemiepiphytes, and climbing plants. Tree fern trunks provide both suitable establishment surfaces for a range of woody epiphytes and hemiepiphytes in New Zealand, as well as attachment surfaces for climbing rātā (*Metrosideros* spp.). We collected detailed occurrence and cover data of woody epiphytes (including hemiepiphytes), climbing rātā, and skirts from 350 *Cyathea smithii* and 350 *Dicksonia squarrosa* across New Zealand. We also collected frequency data on epiphyte, climbing rātā and skirt occurrence from an additional 1212 tree ferns. While skirts reduce the density of woody epiphytes on tree fern trunks, they neither prevent woody epiphytes from establishing on trunks nor prevent epiphytes establishing and growing on areas of the trunk covered by skirts. Envelopment of the growing crown of tree ferns was not observed in any of the 1912 individuals surveyed; incidental observations suggest that climbing rātā crown-envelopment is extremely rare and may occur only when tree ferns are exposed in high-light environments. Tree fern skirts occur on species that are frost-tolerant and occur more frequently in higher elevations and latitudes than non-skirted species. We suggest a new defence hypothesis: skirts protect the growing meristem from freezing conditions.

Keywords: competition, climbing plant, epiphyte, establishment surface, hemiepiphyte, regeneration, growing crown damage, necromass

Introduction

Tree ferns are a prominent feature of many tropical and southern warm temperate forests (Page & Brownsey 1986; Brock et al. 2016; AVH 2020; Manaaki Whenua - Landcare Research 2020), and in New Zealand and south-eastern Australia tree ferns also occur in regions that regularly experience sub-zero temperatures (Wiser et al. 2011; Brock et al. 2016; Fedrigo et al. 2019). In several taxa, dead fronds or frond stipes are retained in a fringe, encircling the top of the trunk of the tree fern like a skirt. Some tree ferns retain thick layers (up to 50 cm deep; JB, unpubl. data) of complete fronds that are retained on the trunk for long periods (decades) of time, e.g. on *Dicksonia fibrosa* (Page & Brownsey 1986; Large & Braggins 2004). The function of these skirts is unknown; however, Page and Brownsey (1986) hypothesised that they function as a physical deterrent to large, woody epiphytes (presumably including hemiepiphytes) and climbing rātā (*Metrosideros* spp.). According to this hypothesis, the benefit to tree ferns of skirts would be that the trunk of the tree fern is subjected to less damage from epiphyte roots, and the growing crown of the tree fern is not enveloped and restricted by the growth of climbing plants (crown-envelopment). Tree fern species with skirts (e.g. *Cyathea smithii*), however, occur alongside tree fern species that predominantly do not have a skirt (e.g. *C. dealbata, C. medullaris*). Further, *D. squarrosa* has an irregular skirt of varying dimensions across the country (Large & Braggins 2004). If the suppression of epiphytes, hemiepiphytes and climbing rātā by skirts is a selective trait, then why do not all tree fern species have skirts, and why do some tree ferns only irregularly have skirts (Pope 1926; Brock et al. 2016)? Further, non-skirted tree ferns do not appear to have any alternative mechanisms for suppressing epiphytes.

Tree fern trunks provide suitable establishment surfaces for epiphytes and hemiepiphytes, and surfaces for climbers to attach to (Pope 1926; Ashton 2000; Rivière et al. 2008; Gianoli 2015). Other than *Weinmannia*-tree fern communities (Wyse et al. 2018), however, the density of epiphytic establishment on tree ferns in the understorey is low, so damage from woody epiphytes may not be a significant risk for individual tree fern survival (Brock & Burns 2021; Veblen & Stewart 1980; Gaxiola et al. 2008). Furthermore, although some species of epiphyte frequently establish close to the growing crown (e.g. *Pseudopanax* spp; Dawson 1986), many woody epiphytes regenerate closer to the base of the trunk (Ogden et al. 1986; Bellingham & Richardson 2006; Gaxiola et al. 2008).

Few studies, however, have examined the impact of epiphytes on tree fern survival. The only previous work on this subject is Bowkett (2011), who studied epiphytes on *Dicksonia antarctica* in the forest understorey of north-eastern

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Tasmania. Bowkett (2011) showed that woody epiphytes appeared not to negatively affect tree ferns, even when they had established near the crown and their roots had embedded themselves into the tree fern trunk.

Our study had two aims:

(1) To critically evaluate the hypothesis of Page and Brownsey (1986) that the function of the tree fern skirt is to reduce the numbers of epiphytes establishing near the crown and overtopping it, or having the crown enveloped by climbing plants thereby damaging the health of the fern.

(2) To determine the patterns and potential drivers of skirt occurrence by comparing skirt occurrence, skirt cover, epiphyte/hemiepiphyte density, and climbing rātā occurrence along a latitudinal (and therefore environmental) gradient.

We chose to study *Cyathea smithii* and *Dicksonia squarrosa* as they occur the full length of New Zealand and both have skirts, although in *D. squarrosa*, this trait is irregular (Lehmann et al. 2002; Large & Braggins 2004; Brock et al. 2016). Field surveys were undertaken along a latitudinal gradient across New Zealand to establish the proportion of tree ferns supporting woody epiphytes and climbing rātā, how extensive any skirt cover was, and to identify any patterns in the occurrence of skirts in *D. squarrosa*.

Although we initially intended to include *Dicksonia fibrosa* in this study, we ultimately did not consider this species for practical, and ecological reasons:

(1) the skirt on this species frequently covers the entire trunk almost completely, reducing the available establishment area for epiphytes (zero epiphytes and climbers were recorded during the first 75 individuals examined). The relationship between skirts and epiphytes was therefore not contested.

(2) this species is not as common, or as widespread as *C. smithii* and *D. squarrosa*, and is therefore more challenging to locate in survey areas where the other two taxa co-occur. Nevertheless, we made incidental records when we observed epiphytes and climbing rātā growing on *D. fibrosa*.

Methods

Field surveys

We recorded occurrences of epiphytes (hereafter including hemiepiphytes), climbing rātā species (*Metrosideros* spp., Myrtaceae) and skirt structures on *Dicksonia squarrosa* (Dicksoniaceae) and *Cyathea smithii* (Cyatheaceae). Seven forests supporting these species from the Mataraua Plateau near Waipoua (35°36′51″S 173°37′54″E) to Te Wharawhara (Ulva Island) (46°55′48″S 168°07′22″E) were surveyed (Table 1; Brock & Burns 2021). At each of these locations, multiple 100 m transects were laid along access paths into the forest interior. Following a point-centred quarter (PCQ) method at regular < 20 m spacing to select individuals (Mitchell 2015), 50 individuals of each species that were greater than two metres in trunk height (epiphytes absent on shorter-trunked tree ferns), and had woody epiphytes present, were identified and sampled (a total of 700 tree ferns).

The height and diameter at breast height (DBH) were recorded for every tree fern. To describe the proportion of trunk covered by any skirt, four measurements of skirt length were recorded (on each of the cardinal directions) along with an estimate of skirt cover (0 = 0%, 1 = 1–24%, 2 = 25–49%, 3 = 50–74%, 4 = 75–100%). Mean skirt length, trunk height, and DBH were used to calculate values of skirt area, trunk surface area, and thereby proportional cover of trunk by skirt, i.e. how much of the trunk surface was obscured by the skirt. The vertical position (height up tree fern trunk) of every woody epiphyte on each tree fern was recorded, and whether the epiphyte was a seedling (<135 cm tall), sapling (>135 cm tall), or tree (>2.5 cm DBH). Those woody epiphytes that established underneath / in the extent of the skirt were identified to species level. The occurrence of climbing rātā in the skirt, or around the canopy of tree ferns was also recorded. Any evidence of damage to the trunk or growing crown was recorded. Species names follow Ngā Tipu o Aotearoa (https://ltl.lincoln.ac.nz/nga-tipu-o-aotearoa-new-zealand-plants/).

To establish the frequency of occurrence of skirts, woody epiphytes, and climbing rātā, a second set of 100 m transects were run into the forest on random bearings avoiding edges, and at regular 15 m intervals along these transects, the PCQ method was again used to identify a minimum of 50 individuals of each of the two tree fern species. The presence of woody epiphytes, climbing rātā, and skirts was recorded on each of these tree ferns to establish the relative proportions of their inter-relationships.

Further, where incidental observations were made of a climbing rātā enveloping the growing crown of a tree fern, a record was kept of whether or not the tree fern had a skirt, and notes on the habit and habitat of the tree fern were made.

Table 1. Latitudinal distribution of survey area, percentage of tree ferns supporting epiphytes in skirts and climbing rātā on the trunk at each area, percentage of tree ferns of each species at all sites that have skirts, and mean proportional skirt cover of trunk (± 1 SD).

Area	Latitudinal range of survey sites (decimal °S)	Percentage of tree ferns supporting		Percentage of tree ferns with skirts		Mean percentage skirt cover of trunk	
		epiphytes in skirts	climbing rātā	*Cyathea smithii*	*Dicksonia squarrosa*	*Cyathea smithii*	*Dicksonia squarrosa*
Waipoua	35.61–35.66	1.0	33.5	100	8	70 ± 25	0 ± 1
Coromandel	37.12	15.0	38.7	100	4	61 ± 24	1 ± 2
Rotorua	38.03–38.09	14.0	59.5	100	6	73 ± 18	2 ± 4
Palmerston North	40.12	49.0	45.8	100	10	66 ± 32	33 ± 34
Nelson	40.85–41.30	12.0	52.4	100	83	68 ± 27	34 ± 37
Moana	42.64–42.69	16.0	59.6	100	86	71 ± 31	14 ± 23
Rakiura	46.86	34.4	56.9	100	91	72 ± 32	36 ± 34

Finally, we made incidental observations of epiphytes and climbing rātā on *D. fibrosa*, as the tree fern species with the largest and most persistent skirt, where they were noted during field surveying work.

Statistical analysis

We used a generalised linear model with Gaussian errors and survey area as a random effect to establish the relationship between the trunk skirt cover and woody epiphyte density. To identify patterns between woody epiphyte or climbing rātā occurrence, and skirt occurrence we used chi-square on a frequency table of epiphytes presence / absence, rātā presence / absence, and skirt presence / absence.

Analysis was undertaken in R studio v1.0.143 (R Core Team 2015) and used the package lme4 v1.1-23 (Bates et al. 2015).

Results

Woody epiphyte density on tree fern trunks (as a function of the entire trunk surface area) was negatively related to the proportion of the trunk covered by skirts ($t = -6.631$, $P < 0.0001$). The mean (± 1 SD) density of woody epiphytes on tree ferns with a skirt that covered less than 5 % of the trunk ($n = 258$) was 0.38 ± 0.39 m^{-2} compared to the density of woody epiphytes on tree ferns with a skirt that covered more than 50% ($n = 306$) of the trunk at 0.02 ± 0.22 m^{-2}. However, epiphytes were recorded as growing on trunk surfaces under skirts on 35% ($n = 124$) of the *C. smithii* trunks, and 79% ($n = 85$) of the *D. squarrosa* trunks where individuals had skirts covering more than 10% of the trunk (108 of 350 surveyed). Overall, 19% of the woody epiphytes ($n = 641$) encountered on tree fern trunks occurred within the area of the trunk covered by the skirt (17 ± 20% of the trunk). Saplings that were identified as establishing underneath / growing from trunks beneath tree fern skirts included: *Coprosma autumnalis*, *Geniostoma ligustrifolium*, *Griselinia littoralis*, *Melicytus ramiflorus*, and *Schefflera digitata* (Table 2, Fig. 1).

Although 52.5 ± 8.4% tree ferns supported various species of climbing rātā (*Metrosideros albiflora*, *M. diffusa*, *M. fulgens*, *M. perforata*) as well as hemi-epiphytic rātā (*Metrosideros robusta*, *M. umbellata*), only three tree ferns had climbers in their skirts, and none of the 1912 tree ferns surveyed had climbing rātā enveloping their crowns. The complete envelopment of a crown of a tree fern by climbing rātā appears to be rare. During the survey work, we observed nine tree ferns with rātā having enveloped the crown of the

Figure 1. Seedling of *Coprosma autumnalis* (Rubiaceae) growing from beneath the dense skirt of a 2.5 m tall *Dicksonia fibrosa* (near Rotorua, Bay of Plenty, New Zealand).

Table 2. Species of epiphyte seedlings and saplings (> 135 cm) recorded as having established underneath/were growing from trunks beneath tree fern skirts.

Epiphyte species	**Waipoua**	**Coromandel**	**Rotorua**	**Palmerston North**	**Nelson**	**Moana**	**Rakiura**	***Cyathea smithii***	***Dicksonia squarrosa***	**Seedling in skirt**	**Sapling in skirt**
Aristotelia serrata				×		×	×	×	×	×	
Beilschmiedia tawa	×			×				×	×	×	
Brachyglottis repanda				×				×		×	
Brachyglottis rotundifolia							×	×		×	
Carpodetus serratus		×					×	×		×	
Coprosma areolata							×	×		×	
Coprosma autumnalis		×	×	×	×	×	×	×	×	×	×
Coprosma foetidissima							×	×	×	×	
Coprosma lucida		×	×			×	×	×	×	×	
Coprosma robusta		×						×		×	
Dacrycarpus dacrydioides				×					×	×	
Dracophyllum longifolium							×		×	×	
Fuchsia excorticata							×	×		×	
Geniostoma ligustrifolium		×	×	×				×	×	×	×
Griselinia littoralis						×	×	×	×	×	×
Hedycarya arborea		×		×		×		×	×	×	
Knightia excelsa		×	×	×				×	×	×	
Kunzea robusta		×						×		×	
Melicytus ramiflorus		×	×	×	×	×		×	×	×	×
Metrosideros umbellata					×		×	×	×	×	
Myrsine australis							×	×	×	×	
Myrsine salicina		×						×		×	
Olearia rani		×						×		×	
Pennantia corymbosa							×		×	×	
Phyllocladus trichomanoides		×						×		×	
Piper excelsum				×					×	×	
Pittosporum huttonianum		×						×		×	
Pittosporum tenuifolium							×		×	×	
Podocarpus totara							×		×	×	
Pectinopitys ferruginea							×		×	×	
Pseudopanax arboreus		×	×	×	×			×	×	×	
Pseudopanax colensoi						×		×		×	
Pseudopanax crassifolius		×		×			×	×	×	×	
Quintinia serrata						×		×		×	
Raukaua edgerleyi						×	×	×	×	×	
Schefflera digitata		×	×	×		×	×	×	×	×	×
Weinmannia racemosa			×		×	×	×	×	×	×	×
Weinmannia sylvicola		×						×	×	×	

tree fern; all but two individuals (*Cyathea medullaris*) had substantial skirts, and all were in high-light environments (canopy gaps, open vegetation; Table 3), where the tree fern growing crown was emergent from the canopy / surrounding vegetation. No obvious damage to the trunks or growing crowns was recorded during the survey.

The chi-squared analyses of the frequency of woody epiphyte presence and climbing rātā presence by skirt cover classes (0-4) did not indicate that the presence of woody epiphytes or climbing rātā were affected by the presence or extent of cover of a skirt. Unexpectedly, however, woody epiphytes were more frequently absent ($X^2_{(df = 4,\ n = 1212)} = 21.025$, $P = 0.0003$) where skirts were absent. There were no associations between skirt occurrence, or cover and the presence of climbing rātā.

Although *C. smithii* consistently had a skirt at all surveyed locations, *D. squarrosa* had varied skirt presence along the latitudinal gradient – with significantly fewer individuals ($X^2_{(df = 32,\ n = 612)} = 352.99$, $p < 0.0001$) with skirts at Waipoua (8%) compared to those individuals on Rakiura (91%) (Table 1).

Skirt-coverage of *C. smithii* trunks was relatively consistent across the country with a mean (± SD) cover = 69 ± 30% of trunks. In comparison, skirt coverage of *Dicksonia squarrosa* trunks was lower overall (17 ± 29%) and cover was more varied across the country. Skirt cover for *D. squarrosa* was recorded as zero at Waipoua (although 8% of individuals retained one or two dead stipes, their cover values were so low as to be negligible) in the north of the country, and at 36 ± 34% of trunks in Rakiura in the south (Table 1).

Only two of 175 *D. fibrosa* were observed supporting climbing rātā during our survey. Also, five *D. fibrosa* were identified as supporting woody epiphytes including *Coprosma autumnalis* and *Weinmannia racemosa* from underneath their skirts. *Coprosma autumnalis* was always recorded growing from the top of the trunk from between the dead fronds of the skirt (Fig. 1).

Table 3. Incidental observations of tree ferns with climbing rātā enveloping their growing crown.

Species of tree fern	Skirt present?	Trunk height (m)	Location	Description of site
Cyathea smithii	Y	3.5	Tōtaranui, Abel Tasman National Park	On edge of campsite, open area with tree fern in canopy; exposed
Cyathea smithii	Y	4	Oban, Rakiura	On bank above road; on forest margin; isolated and exposed
Cyathea smithii	Y	3	Waikaremoana Track	On stream bank adjacent to campsite; isolated and exposed
Dicksonia fibrosa	Y	4.5	Lake Okataina Scenic Reserve, Rotorua	In grassland in centre of frost flats; isolated and exposed
Dicksonia fibrosa	Y	4	Lake Okataina Scenic Reserve, Rotorua	In grassland in centre of frost flats; isolated and exposed
Dicksonia squarrosa	Y	3	Papatowai, Southland	On grassy road verge adjacent to grazing field; isolated and exposed
Dicksonia squarrosa	Y	3.5	Oban, Rakiura	In drainage ditch on side of road; isolated and exposed
Cyathea medullaris	N	5	Hūnua Ranges	Low canopy; on edge of a landslide; tree fern exposed
Cyathea medullaris	N	6	Hūnua Ranges	Low canopy; tree fern canopy emergent, and exposed

Discussion

We have collected a robust dataset to examine the hypothesis that tree fern skirts reduce the establishment of woody epiphytes and/or climbing rātā thereby protecting the long-term health of the tree fern. Although the presence of a skirt encircling the growing crown of a tree fern does reduce the density of woody epiphytes over the surface of the entire trunk (i.e. reduces establishment area for some species), skirts (even those as extensive and thick as on *D. fibrosa*) do not prevent woody epiphytes from establishing at the top of the trunk. Furthermore, there appears to be no association between woody epiphyte and/or climbing rātā occurrences and skirt occurrence; interestingly there were significantly fewer woody epiphytes where skirts were absent. None of the 1912 tree ferns surveyed exhibited crown or trunk damage, or had their crowns enveloped in the growth of a climbing rātā.

Where tree ferns were observed incidentally as being enveloped by climbing rātā, they were all present in modified landscapes, or in recently disturbed areas (landslide / canopy gap). Further, all nine of these tree ferns had full skirts, with the exception of *C. medullaris,* which did retain a few large, dead fronds. This pattern suggests, along with the lack of any climbing rātā crown-envelopment data from the survey, that not only is the problem of climbing rātā crown-envelopment a relatively rare one for tree ferns, but that when it does occur it is only in specific conditions. Possibly, crown-envelopment may occur only in high-light conditions due to the significantly increased light levels compared to those experienced by climbing rātā in the understorey, enabling the climber to develop faster than the tree fern (Gianoli 2015). The Page & Brownsey (1986) hypothesis is that skirts on tree ferns act to suppress the establishment of woody and climbing epiphytes that might damage the trunk or envelop and damage the crown. Our evidence suggests that at a tree fern population-level, the presence of a skirt may reduce the density of woody epiphytes; but that at an individual level, the physical presence of a skirt does not prevent woody epiphytes from establishing and growing near the crown (Fig. 1), even from underneath the skirt. Furthermore, there appears to be no relationship between skirt presence and the presence of climbing rātā on tree fern trunks. Further evidence to test this hypothesis could be gained from more observational and experimental work. For example, the survival of enveloped and free individual tree ferns with and without skirts could be followed (although this may take a considerable period of time), or the comparative growth patterns (as an indication of health) of tree ferns of similar size both with, and without large woody epiphytes growing near their crown examined (as Bowkett 2011).

In terms of skirt structure and occurrence, both *C. smithii* and *D. fibrosa* can be described as consistently skirted tree ferns as almost every individual will have a skirt of some form. However, at a population scale there will be exceptions, and as with *C. smithii*, *D. fibrosa* has been observed with almost no skirt (2.2 m tall and one dead frond) by the authors during field surveys (Kauaeranga Valley).

The *D. fibrosa* skirt is clearly the most developed, extensive and consistent of any tree fern species in New Zealand. It is almost always complete (100% cover of the upper portion of the trunk), can be over 50 cm deep (layer of dead fronds from trunk to outer surface of skirt), and covers a larger proportion of the trunk structure compared to *C. smithii* and *D. squarrosa*. However, even though woody epiphytes were rarely recorded on *D. fibrosa* (5 instances across 175 individuals), even skirts of the size found in *D. fibrosa* do not prevent woody epiphytes from establishing around the growing crown (Fig. 1). In contrast, *D. squarrosa* is irregularly skirted as it retains no skirt structure at all in warmer northern climates, yet almost always has a skirt that covers over one-third of its trunk in southern, colder climates. *C. smithii* and *D. fibrosa* occur at higher elevations and latitudes than other trunked tree fern species, and are resilient to freezing (Warrington & Stanley 1987; Bannister 2003). Furthermore, *D. fibrosa* is characterised by its ability to establish on forest margins, and in other frost-prone areas (Wardle 1991; Bystriakova et al. 2011). As discussed above, the irregular skirts of *D. squarrosa* increase in occurrence and cover with increasing latitude and corresponding decreases in temperature. If we compare the number of individual tree ferns that experience sub-zero conditions across New Zealand (Wardle 1991; Wiser et al. 2011) to the number of individuals that likely experience damage from epiphytes and climbers, it is possible that more individuals are at risk from freezing conditions than structural damage by colonising plants. Similarly, low temperatures are likely a greater pressure on survival of tree fern populations than the rare potential damage incurred from rātā crown-envelopment or epiphyte growth.

Dense arrays of dead leaves or leaf parts (a necromass; Monteiro & Körner 2013) encircling the growing meristem may provide thermal insulation from freezing (as for Andean plants; Goldstein & Meinzer 1983; Squeo et al. 1991; and in cold-resilient grasses; Monteiro & Körner 2013). This strategy of retaining necromass might permit tree ferns with their tropical growth form to capture cooler space in New Zealand's southern climes. As to Page and Brownsey (1986), our data support the hypothesis that skirts on tree ferns limit the colonisation of trunks by epiphytes and climbing rātā, although identify no patterns indicative of long-term damage of the presence of these colonisers to tree fern health. However, we suggest an alternative hypothesis as to why tree ferns retain dead-frond skirts: skirts may protect the meristem from freezing and are an adaptation that has allowed some tree fern species to extend their distributions into cooler climatic conditions. Further work to establish the robustness of this alternative hypothesis should include experimental examination of the insulation capabilities of tree fern skirts, as well as an analysis of the distribution of different tree fern taxa (with and without skirts) along temperature gradients.

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Author contributions

JB and BB conceived the project idea, survey work was coordinated and undertaken by JB & BB. Analysis and writing were undertaken by JB and reviewed by BB.

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